Pedobiologia **25**, 175—185 (1983)

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A long term study of life cycles and population dynamics of *Tullbergia yosii* and *Onychiurus decemsetosus* (Collembola) in a pine forest soil

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With 6 figures

(Accepted: 82-10-24)

1. Introduction

In recent ecological studies, Collembola have received increasing attention because of their importance in soil formation and litter decomposition processes. A knowledge of life cycles and population dynamics of Collembola is fundamental to provide further understanding of the role of collembolan populations in such soil processes.

Life cycles of field populations have been demonstrated for many species of Collembola by analysing the size or age structures of populations (e.g. Joosse 1969, Fjellberg 1975, Gregoire-Wibo 1979, Addison 1981 and Hudson 1981).

In Japan, there are some studies on the life cycles of collembolan populations in the field, such as, *Folsomia octoculata* Handschin (Takeda 1973, Niijima 1971, 1975, and Tamura 1976), *Tetracanthella sylvatica* Yosii [Takeda 1976], *Isotoma carpenteri* Boerner, *Isotoma sensibilis* Tullberg, *Sinella dubiosa* Yosii and *Tomocerus varius* Folsom [Takeda 1979a] and *T. varius* [Niijima 1975].

This paper, the sixth of a series dealing with the ecology of collembolan populations in a pine forest soil, describes the life cycles and population dynamics of *Onychiurus decemsetosus* Yosii and *Tullbergia yosii* Rusek, over a 11 year period from 1971 to 1982 (Takeda 1973, 1976, 1978, 1979a, b & c).

2. Study area and sampling methods

The study was carried out in a natural forest of Japanese red pine (*Pinus densiflora* Sieb. *et* Zucc.) mixed with *Chamaecyparis obtusa* Endle. at the Kamigamo Experimental Forest Station of Kyoto University, about 12 km north of the centre of Kyoto City (+35.04′ N and 135.43′ E). Details of the study area have been reported in Takeda (1976).

Meteorological data were obtained from the forest station (Kyoto University Forest 1975 and 1980). The mean air temperature over the 11 year period ranged from +3.3 °C (January) to 28.2 °C August). Soil temperature at 10 cm in depth ranged from +4.7 °C (January) to 28.5 °C (August). The mean annual precipitation and evaporation were 1,678 mm and 985 mm respectively. In this study area, the summer precipitation was high but due to high evaporation caused by high temperature and the low water holding capacity of the soil, summer droughts occurred in 1971, 1972, 1973, 1977, 1978, and 1979.

Soil samples were taken from a plot of 10×10 m divided into twenty sub-plots each 1×5 m. During the period from July 1971 to June 1982, with the exception of 1976 and 1977, sampling was carried out at about monthly intervals. In 1977, no sampling was carried out and in 1976, only the October's sample was taken. Soil samples consisted of soil cores each 25 cm^2 in surface area and 4 cm deep (100 cm^3 in volume) and the number of soil cores taken varied from 12 to 25 cores for each sampling occasion.

Soil animals were extracted by a high gradient canister extractor (Macfadyen 1961) at a constant temperature of 35 °C in a cabinet. The period of extraction was six days for all soil samples. The extraction efficiency of this extractor was tested by comparing the extractor extraction and hand-sorting methods (Takeda 1979c). The estimated extraction efficiency was 52.5 % and 75.9 % for *T. yosii* and *O. decemsetosus* respectively. The low extraction efficiency obtained was due to

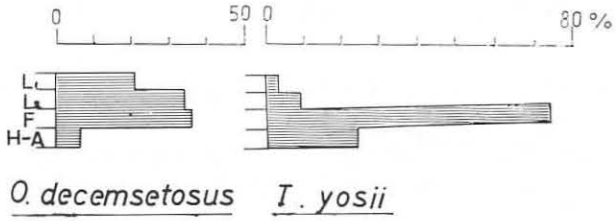


Fig. 1. Vertical distribution of *T. yosii* and *O. decemsetosus*. (L1) New litter layer; (L2) old litter layer; (F) F-layer; (H-A) H-A layer.

the insufficient extraction of juvenile individuals by this extractor. The identification, counting and measurement were undertaken under a binocular microscope with a micrometer. The animals collected during the period from July 1972 to May 1975 were grouped into size classes according to their body length. Besides the grouping of body length classes, the development of the genital apertures was examined in the animals collected during the period from July 1974 to May 1975. According to the morphology of the genital apertures, the animals were divided into adults and juveniles and the sex was determined for the adult individuals.

Animals collected in the study area were used for observation of breeding biology and post-embryonic development of the two species. The animals were kept in glass tubes each 1 cm in diameter and 3 cm in height filled to a depth of 1 cm with a charcoal-plaster mixture. Animals were fed on commercial bakers yeast. Rearing was carried out at 25 °C.

3. Notes on the species studied

Onychiurus decemsetosus Yosii was originally described by Yosii from the specimens collected in Nepal (Yosii 1966). *Tullbergia yosii* Rusek was described by Rusek (1967) based on specimens collected from China. This species is a member of the cosmopolitan *Tullbergia krausbaueri* group which is abundant in various soils in European countries (Rusek 1971).

The species and abundance of the collembolan fauna in this study area during 12 sampling occasions from June 1974 to May 1975 has been shown by Takeda & Ichimura (1983; Table 1). Collembolan fauna in this area consisted of 36 species; among them *T. yosii* and *O. decemsetosus* accounted for 24.2 and 3.6 % respectively of the total population.

The vertical distribution of 10 species of Collembola have been studied in this study area and *T. yosii* and *O. decemsetosus* have a mode of vertical distribution within 1—3 cm and 0—2 cm in depth respectively (Takeda 1978). In this study, the vertical distribution of the two species was re-examined in relation to the soil profile and the results are shown in Fig. 1. Both species were abundant in the F layer but had a different mode of distribution. The micro-distribution of ten species of Collembola have been studied in this study area and the two species showed an aggregative distribution (Takeda 1979c). The degree of aggregation was lower in *T. yosii* than in *O. decemsetosus* populations.

4. Results

4.1. Laboratory observations on life history

4.1.1. Tullbergia yosii

Observations were made on 5 individuals reared in separate jars. At 25 °C the development of the eggs took 15—17 days and the mean instar duration was 3.6, 3.0, 4.5 and 6 days for first, second, 3rd, and 4th instars respectively. Sexual maturity was attained at the 3rd instar, 6.6 days after hatching. Adult individuals reared in isolation laid one to 2 eggs at each oviposition, indicating parthenogenetic reproduction in *T. yosii*.

4.1.2. Onychiurus decemsetosus

Development of eggs took 10 days at 25 °C and one egg batch consists of 3—10 eggs. For this species, the duration of each instar was not observed, but the body lengths of the ten individuals were measured at 3 days intervals from hatching to sexual maturity. The animals were sexually mature 33 days after hatching at 25 °C.

4.2. Size distribution and sex ratio in the field populations

Collembola have no marked metamorphosis and they grow by a series of moults which continue throughout life so it is difficult to interpret the age of individuals in terms of instar classes for the natural populations. Consequently, body length was used instead of age.

The size distributions are shown in Fig. 2. The range of body length in adult females and males completely overlap the distributions but the mean length of females was longer than that of males in the case of *O. decemsetosus* ($P < 0.001$). For *T. yosii*, 1,710 individuals were examined. All were females and this suggests parthenogenesis in this species. This reproduction pattern was also supported by laboratory observations. The sex ratio obtained for *O. decemsetosus* was 1 : 2.6 for male to female and was significantly different from 1 : 1 sex ratio ($P < 0.01$). The biased sex ratio has often been observed in field populations of Collembola and has been explained by different mortality patterns for the two sexes (Takeda 1976 and Petersen 1978).

4.3. Life cycles of the two species in the field

4.3.1. General

Size distribution and population densities throughout the period from July 1972 to June 1975, and from October 1973 to June 1975 for *T. yosii* and *O. decemsetosus* respectively, are shown in Fig. 3. The adults and juvenile individuals were separated by the consideration of Fig. 2.

4.3.2. Tullbergia yosii

The first size class individuals occurred at every sampling date but the proportion in this size group was high in spring and summer populations. The proportion of first size individuals in the population reflects the breeding activities in a time delayed manner because of the egg period. The relation between the proportion of first size individuals and soil temperature at the sampling dates was significantly correlated at $P < 0.001$ (d.f. = 30).

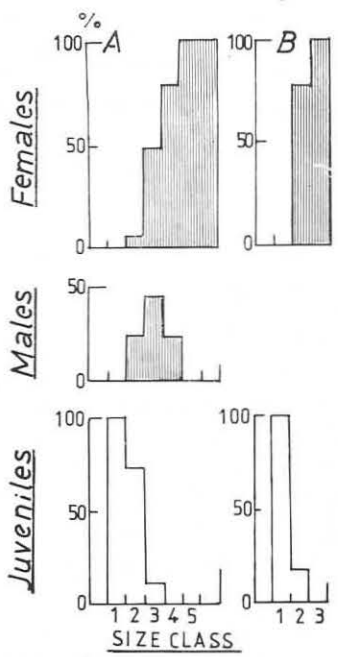
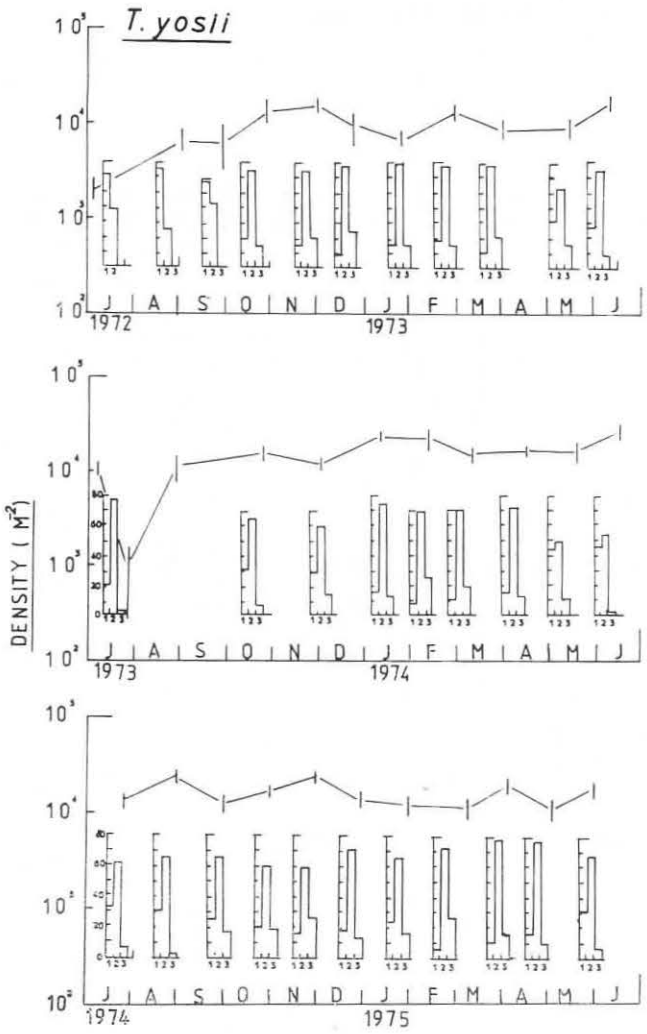


Fig. 2. Size distribution. Animals were divided into 5 size classes: 1st ($\leq$ 0.375 mm), 2nd (0.375—0.500 mm), 3rd (0.500—0.625 mm), 4th (0.625—0.750 mm), and 5th ($\geq$ 0.750 mm). (A) *O. decemsetosus*, (B) *T. yosii*.



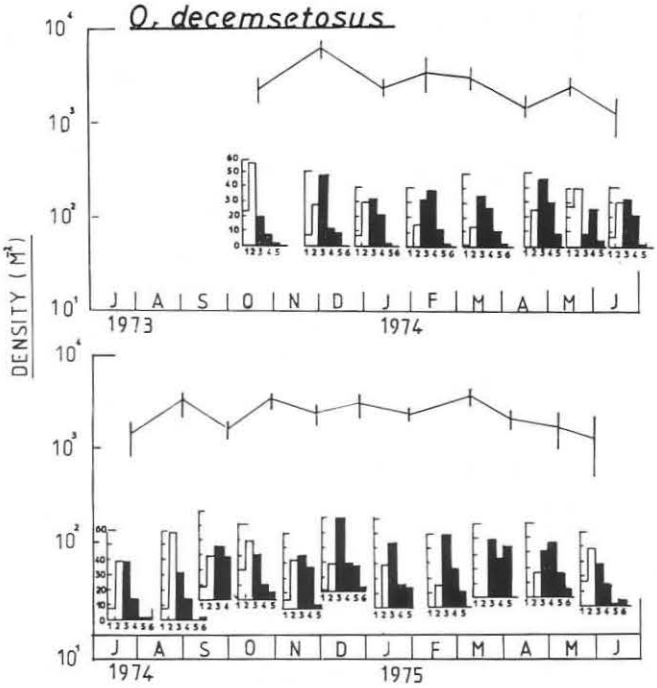
3a

Fig. 3. Seasonal changes in size distribution and population density of **(a)** *T. yosii*, and **(b)** *O. decemsetosus*. Size classes see Fig. 2. Bars indicate the standard errors.

The population of this species did not show any changes in size distribution during the period from December to March. The recruitment and the growth rate of this population decreased in winter. The high percentage of first size individuals in May populations showed the recruitment of juveniles into the population and this spring generation was followed continuously by generations throughout the growth period until December.

4.3.3. Onychiurus decemsetosus

The life cycle was estimated by following the changes in size distribution throughout the study period. Fig. 3 shows that the recruitment took place throughout the year except winter (December to March) as shown by the presence of first size class individuals in the populations. The main recruitment periods were in August, October and May-June as indicated by the high proportions of individuals of the first and second size classes. The individuals appearing in July to August (summer generation) grew into adults by October.



3b

The individuals appearing in late October (autumn generation) grew during autumn, winter and spring and probably attained the adult stage by the following spring. There was a high proportion of first size class individuals in May, suggesting the recruitment of juvenile individuals into the population. The individuals recruited in May/June grew rapidly during spring and early summer and probably produce the summer generation before August. This species had three generations a year, although there was overlapping of the different generations throughout the year.

4.4. Population dynamics

4.4.1. Seasonal abundance of the two species

For the comparison of seasonal abundance between different years, the study period was separated into 8 annual cycles corresponding to each period from July to June.

Seasonal changes in number of *T. yosii* and *O. decemsetosus* during the 8 annual cycles are shown in Fig. 4.

Similarity in seasonal abundance between the two species was examined by using SPEARMAN's rank correlation (SIEGEL 1958) and the results are given in Table 1. Both species showed a similar seasonal abundance during all annual cycles except the 5th and 8th annual cycle. These similarities in seasonal abundance suggest that the two species have similar responses to the seasonal changes in environmental conditions.

For each species, seasonal abundance was compared between the different annual cycles. In the case of *O. decemsetosus*, the patterns of seasonal abundance may be divided into 3 types:

(1) During the 1st and 2nd annual cycles, there was a mid-summer low in numbers with winter and spring peaks. **(2)** During the 3rd, 5th and 6th annual cycles, seasonal abundance showed an unimodal pattern with a peak density in winter. **(3)** During the 4th, 7th and 8th annual cycles, there were no apparent population peaks and the population was rather variable during the period from July to December, with a winter population decrease in numbers.

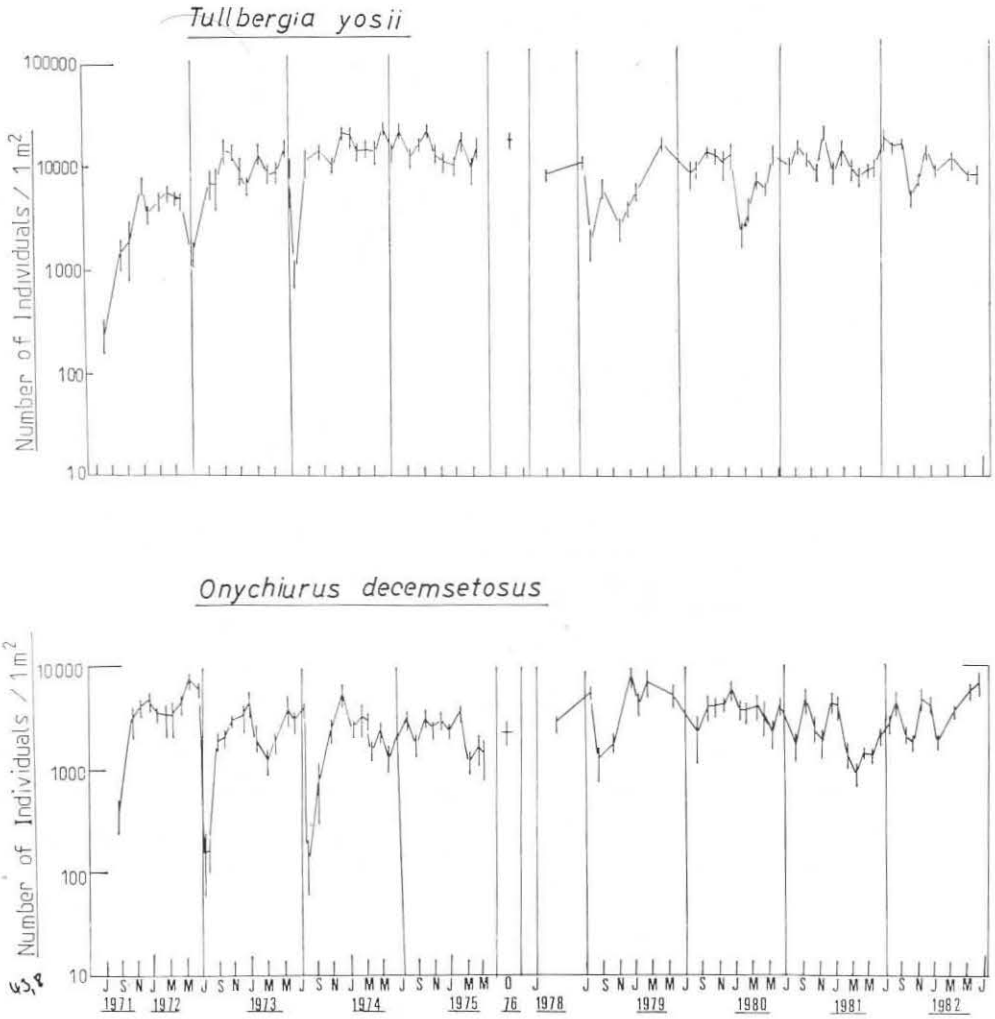

Tullbergia yosii
Number of Individuals / 1 m²
100000
10000
1000
100
10
Onychiurus decemsetosus
Number of Individuals / 1 m²
10000
1000
100
10
J S N J M M J S N J M M J S N J M M J S N J M M J S N J M M O J J S N J M M J S N J M M J S N J M M J S N J M M J
1971 1972 1973 1974 1975 76 1978 1979 1980 1981 1982

Fig. 4. Population density changes of *T. yosii* and *O. decemsetosus* over the study period from July 1971 to June 1982. Bars indicate the standard errors.

Table 1. The similarity between seasonal abundance of *T. yosii* and *O. decemsetosus* over the 8 annual cycles and mean annual population densities and standard errors for 8 annual cycles

Species name	Mean annual population density/1 m² (standard error)							
	1st	2nd	3rd	4th	5th	6th	7th	8th
Onychiurus decemsetosus	3,923 (607)	2,180 (354)	3,008 (460)	2,345 (247)	4,834 (973)	4,023 (326)	2,574 (486)	4,010 (581)
Tullbergia yosii	3,803 (729)	9,677 (1,467)	15,937 (2,352)	16,471 (1,524)	8,215 (2,399)	10,458 (1,460)	13,445 (1,490)	11,374 (1,575)
Rank correlation coefficient	0.768**	0.729**	0.751**	0.654*	0.324	0.580*	0.590*	—0.103

** Significant at $p < 0.01$, * significant at $p < 0.05$.

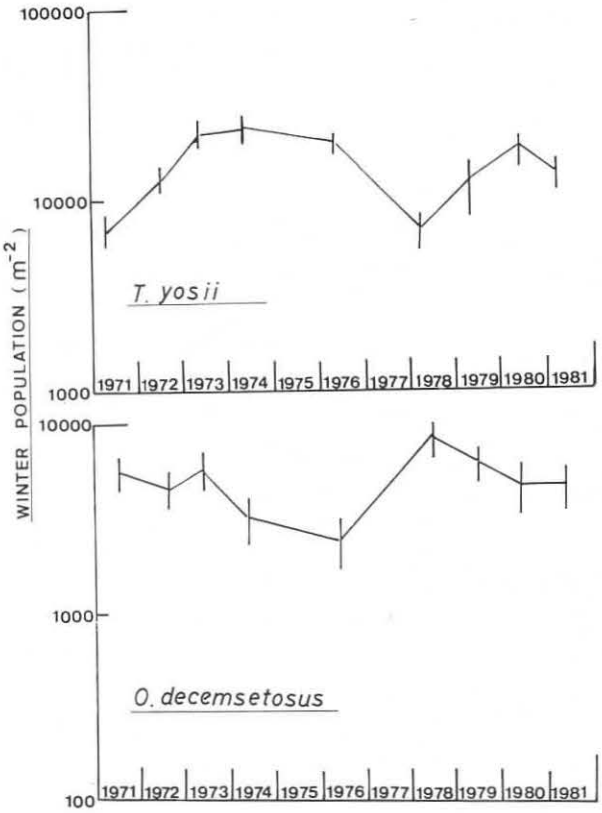


Fig. 5. Winter population density levels over the study period from 1971 to 1982. Bars indicate the standard errors. Winter population density level is the population density before the winter population decrease.

For the *T. yosii* population, seasonal abundance showed a similar pattern in the 1st, 2nd and 3rd annual cycles. During the 4th, 7th and 8th annual cycles, population density was variable through the year. During the 5th annual cycle, the population showed a summer decrease in numbers and then increased during the period from August to May. During the 6th annual cycle, population density was variable during the period from July to January and decreased in winter.

In both species, there was a population decrease in mid-summer during the 1st, 2nd, 3rd, and 5th annual cycles while there were no summer population decreases in the 4th, 6th, 7th and 8th annual cycle, when summer precipitation was higher than in normal years. Summer drought conditions shaped the seasonal abundance patterns of the two species.

4.4.2. Comparison of population density between the 8 annual cycles

The mean population densities ($\pm$ s.e.) are shown for the 8 annual cycles in Table 1. For both species, mean population density was not so different between different years irrespective of the seasonal variations. The recruitment period of both species was from May to December in every year. Thus the population changes during the recruitment period represent the population growth of the species as a result of birth and death processes and the population attains a winter population level. The winter population levels attained by the end of recruitment period were remarkably similar between the annual cycles. The results suggest density dependent regulation in the two populations (Fig. 5).

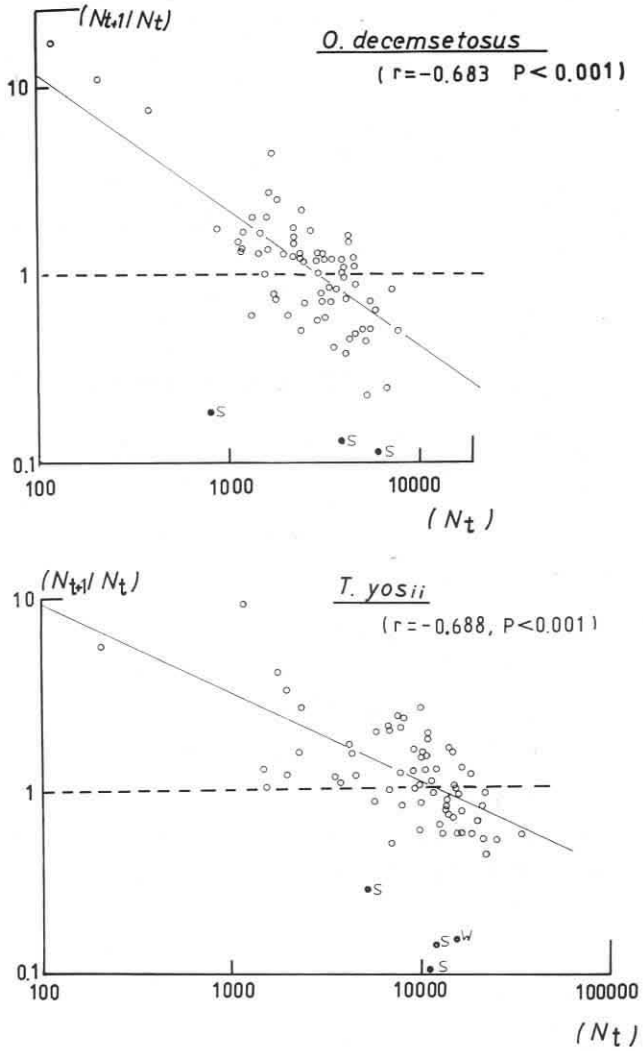


Fig. 6. The relationships between log (N_{t+1}/N_t) and log (N_t). Summer and winter population decreases are indicated by the letter (s) and (w) respectively.

The changes in abundance from one sampling date to the next is expressed by the ratio, (N_{t+1}/N_t) and the $\ln(N_{t+1}/N_t)$ equal to the intrinsic rate of increase per month under the stable age populations (LOTKA 1956). For the successive sampling dates the values of (N_{t+1}/N_t) were calculated and were plotted against the initial density (N_t) to examine the density dependent effects (Fig. 6). The log ratio decreased with the increases of population density and the equilibrium density of each species was 12,300 and 4,000 ind. m^{-2} for *T. yosii* and *O. decemsetosus* respectively. In the case of *T. yosii*, summer population decrease in 1972, 1973 and 1978 and winter decrease in 1980 departed from the regression line. In the case of *O. decemsetosus* summer population decrease in 1972 and 1973 departed from the regression line. The results suggest that the summer population decreases were density independent.

5. Discussion

Patterns of reproduction were different in the two species. Parthenogenesis in *T. yosii* was confirmed in field and laboratory observations. The population of *O. decemsetosus* showed an excess of females and the sex ratio significantly departed from 1 : 1. The excess of females in populations has often been observed in soil Collembola (HÜTHER 1961 and PETERSEN 1978, 1980). PETERSEN (1978) working in a Danish beech forest showed that an excess of females in bi-sexual populations and parthenogenesis were more common in the euedaphic than in epiedaphic and hemiedaphic species. He also related the reproductive strategies of Collembola to the degree of stability of their habitats. In this study, the two species studied were distributed in the F layer and their distribution was deeper than the distribution of surface dwelling species (TAKEDA 1978). The present results may support the view provided by PETERSEN (1978).

Life cycles have been studied for many species of Onychiuridae because of their abundance in various soils. HALE (1980) working in a moorland in England showed that *Onychiurus* spp. had one to two generations a year and the recruitment extended from May to November. TANAKA (1970) studying two species, *Onychiurus* sp. and *Isotoma trispinata* MACGILLRAY, in a warm temperate region in Japan showed that *Onychiurus* sp. had about 4 generations a year. Although there have been no published studies on the life cycle of *T. yosii*, this species is a member of the *T. krausbaueri*-group (RUSEK 1971) and there have been several studies on the life cycle of *T. krausbaueri*. LEINAAS (1978) studies the life cycle of *T. krausbaueri* in a Norwegian forest and found that recruitment took place in spring and summer, and a similar life cycle has been reported for *T. krausbaueri* in a Swedish pasture (PERSSON & LOHM 1978). HUTSON (1981) studying the colonization processes of Collembola in reclamation sites in England noted that *T. krausbaueri* appeared to have only two generations a year.

Life history studies on collembolan species in antarctic and alpine regions have generally shown that the life span of species was usually 1—3 years (JANETSCHEK 1967, FJELLBERG 1978 and ADDISON 1981). In cool and warm temperate regions, the life span of species was from 2—12 months according to the species and habitat studied and the number of generations also ranged from 1—5 generations a year. Even in the same species, the life cycle and life span was variable according to the temperature regime of the habitats (TAKEDA 1974 and TAMURA & MIHARA 1977).

The number of generations a year estimated in this study is reasonable compared with results of other studies. The life cycles of both species were similar and were characterized by a growth and recruitment period from May to December and an arrest of growth and recruitment in winter. The two species showed overlapping generations throughout the year except in winter due to the continuous breeding of adults. Collembola usually show flexible life cycles and even univoltine species there is overlapping of different age groups in the population (FJELLBERG 1978 and ADDISON 1981).

Seasonal changes in number of a certain species depend upon the balance of natality and mortality for populations in which there is no emigration or immigration. Both species had a similar life cycle and this similarity was reflected in the pattern of seasonal abundances of the two species. Two different patterns of seasonal abundance were seen in the 8 annual cycles. In the years with a drought in summer, populations showed a midsummer low in numbers with spring and winter peaks. When there was no drought in summer, population were rather variable throughout the recruitment period and decreased in winter. The summer drought may be responsible for shaping the difference in seasonal abundances between years.

The seasonal abundance was rather variable between years and in the year with the greatest fluctuations (the 3rd annual cycle), population density ranged from 133 to 5,890 ind. m^{-2} and from 1,220 to 23,450 ind. m^{-2} for *O. decemsetosus* and *T. yosii* respectively. In spite of the seasonal fluctuations in population density the two populations were remarkably stable in their winter population levels and the mean annual population density was

not so different between years. These observations can not as yet be fully explained because of the lack of detailed information on population dynamics, especially mortality factors affecting the populations at different times of the year. Some speculation for the stability of the populations may be derived from the present results. The relation between (N_{t+1}/N_t) and (N_t) indicates the density dependent regulation in the populations.

Examination of the results showes that the density dependent regulation works mainly in the increasing phase of population. The sudden population decreases in summer were density independent and were related to the intensity of drought conditions. LEBRUN (1969) studied a population of *Nothrus palustris* and showed density dependent regulation within an increasing population, and a density independent factor for the population decreases.

The values of (N_{t+1}/N_t) above 1 represent population increase per month and realized capacity of population increase. The mean value was 2.116 ($\pm$ 2.000 S.E.) and 1.653 ($\pm$ 0.387 S.E.) for the *O. decemsetosus* and *T. yosii* populations respectively. The realized increase rates were low compared with those of other terrestrial arthropods (SOLOMON 1964 and VARLEY *et al.* 1972). The low increase rate of the populations may be explained by the low number of eggs oviposited in each oviposition as shown in the laboratory cultures.

The two species examined in the present study exhibited iteroparity as shown by the prolonged breeding and overlapping generations throughout the year. The two species inhabited the F layer where the environmental conditions are more moderate than in the surface layer or above ground. The life cycles observed in this study may be a reflection of the stability of the environmental conditions which permit breeding throughout the year with the exception of winter.

6. Acknowledgements

I wish to express my sincere gratitude to Dr. J. ADDISON, Prof. T. TSUTSUMI and Dr. M. LUXTON for their kindness in reading and criticizing the manuscript.

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Synopsis: *Original scientific paper*

TAKEDA, H., 1983. A long term study of life cycles and population dynamics of *Tullbergia yosii* and *Onychiurus decemsetosus* (Collembola) in a pine forest soil. Pedobiologia **25**, 175—185.

The life cycles and population dynamics of two species of Collembola living in a pine forest soil at Kamigamo Experimental Station in Japan were studied between 1971 and 1982. Life history patterns of the two species were similar and were characterized by a recruitment and growth period from May to December and an arrest of recruitment and growth in winter. *O. decemsetosus* YOSII had 3 generations a year and *T. yosii* RUSEK appeared to have more than 4 generations a year. Seasonal abundance was different among the years. In summer drought years, both species showed low number in summer with spring and winter peaks in numbers. In years without drought in summer, the population densities were variable with winter population decreases. In spite of the fluctuations within a year, populations were remarkably stable in the winter and closely comparable between the 8 annual cycles. The stability of population numbers is discussed in connection with the life cycle patterns of the two species.

Key words: Collembola, Tullbergia yosii, Onychiurus decemsetosus, life cycle, population dynamics, seasonal abundance, annual changes, forest soil.